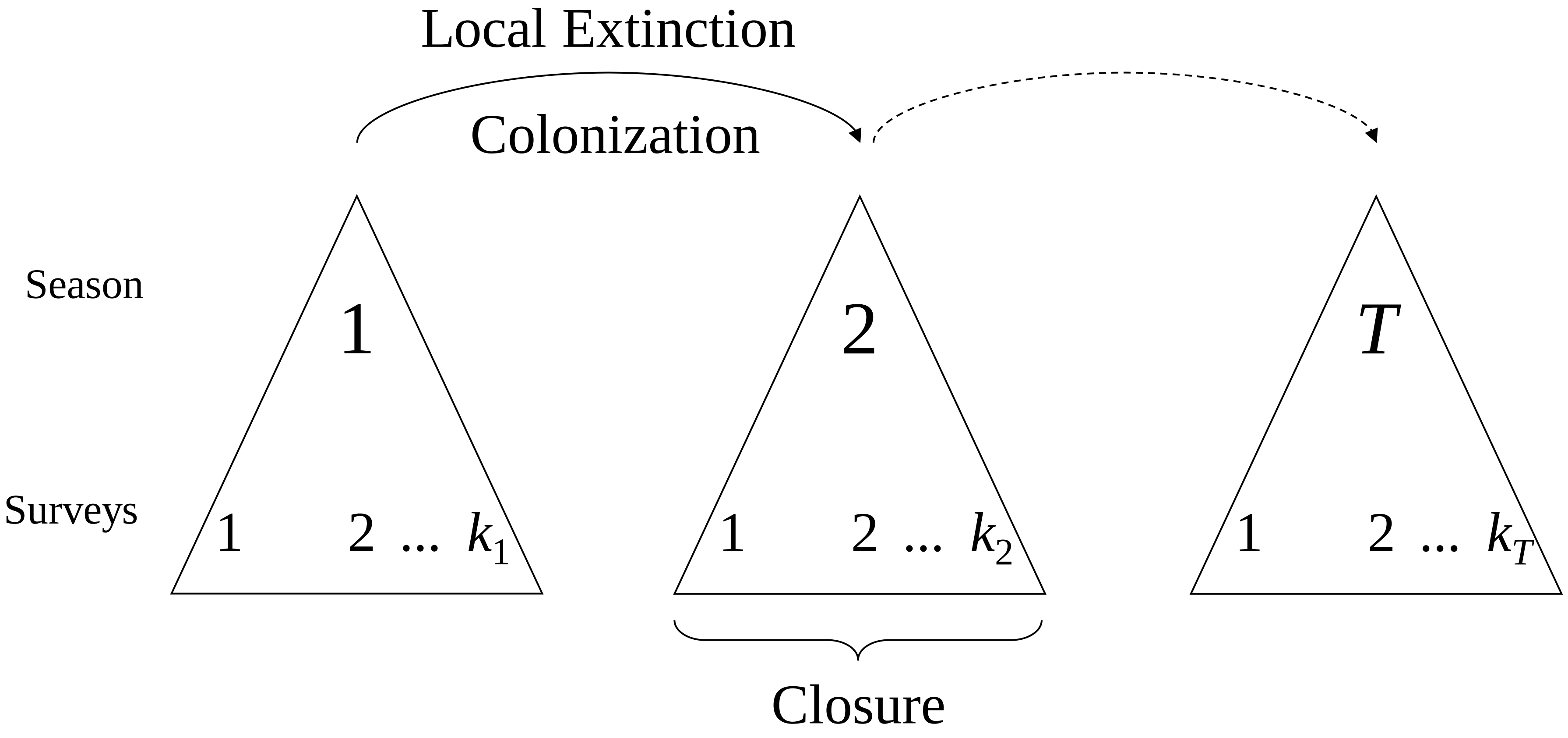
# Multiple Season Model

Part I

# Recap

- From a population of $S$ sampling units, $s$ are selected and surveyed for the species.
- Units are closed to changes in occupancy during a common ‘season’.
- Units must be repeatedly surveyed within a season.
- Units may be surveyed over multiple seasons

# Recap



Local Extinction
Colonization
Season
Surveys
1
1 2 ... $k_1$
2
1 2 ... $k_2$
$T$
1 2 ... $k_T$
Closure

# Recap

| Unit | Season 1 | 2 | … | $T$ |
|---|---|---|---|---|
| 1 | 101 | 001 | … | 011 |
| 2 | 000 | 100 | … | 110 |
| 3 | 100 | 000 | … | 000 |
| . | . | . | … | . |
| . | . | . | … | . |
| . | . | . | … | . |
| . | . | . | … | . |
| $s$ | 000 | 000 | … | 000 |

# Another situation…

- Detection/nondetection data may be collected at a different set of units each season.

# Another situation…

| Unit | Season 1 | 2 | … | $T$ |
|---|---|---|---|---|
| 1 | 101 | | | 011 |
| 2 | 000 | | | 110 |
| 3 | 100 | | | |
| . | | 001 | | |
| . | | 100 | | |
| . | | 000 | | |
| . | | | | 000 |

# How to model multi-season data?

- Consider the data consists of 2 layers
  - true presence/absence of the species each season
  - observed data conditional upon true occupancy state of the site
- Can use either observed or complete likelihood.

# How to model multi-season data?

1. Fit the single-season model to the data from each season
   - Ignores structure and potential information when same units are surveyed over time

2. Fit a model where the dynamic processes of occupancy are explicitly considered
   - Incorporates a form of temporal autocorrelation or heterogeneity in occupancy status of units

# Implicit Dynamics

- Effectively, fit multiple single-season models to the data.
- Can introduce structure to model systematic changes in occupancy.

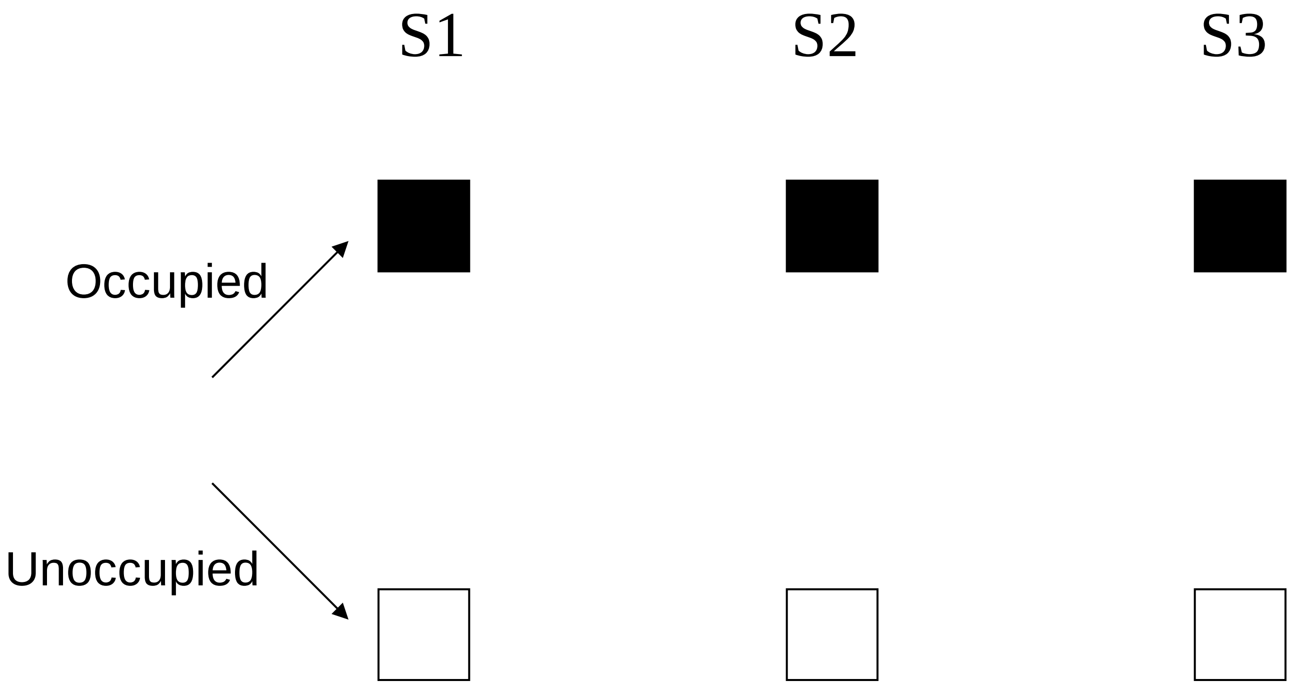
$$\mathrm{logit}\left(\psi_t\right) = \mathrm{a} + \mathrm{b}t$$

- Does not model the dynamic processes of occupancy; local-extinctions and colonizations.
- Implicit dynamics are non-Markovian (random): Pr(occupancy at $t$) is independent of state at $t$ -1.

# Explicit Dynamics

- Barbraud et al. (2003) and MacKenzie et al. (2003) extended the single season model by including parameters for these 2 dynamic processes.
- Model the biological processes of change in occupancy.
- Model occupancy as a first order Markov process: Pr(occupancy at $t$) depends on occupancy state at $t$ -1.

# Explicit Dynamics



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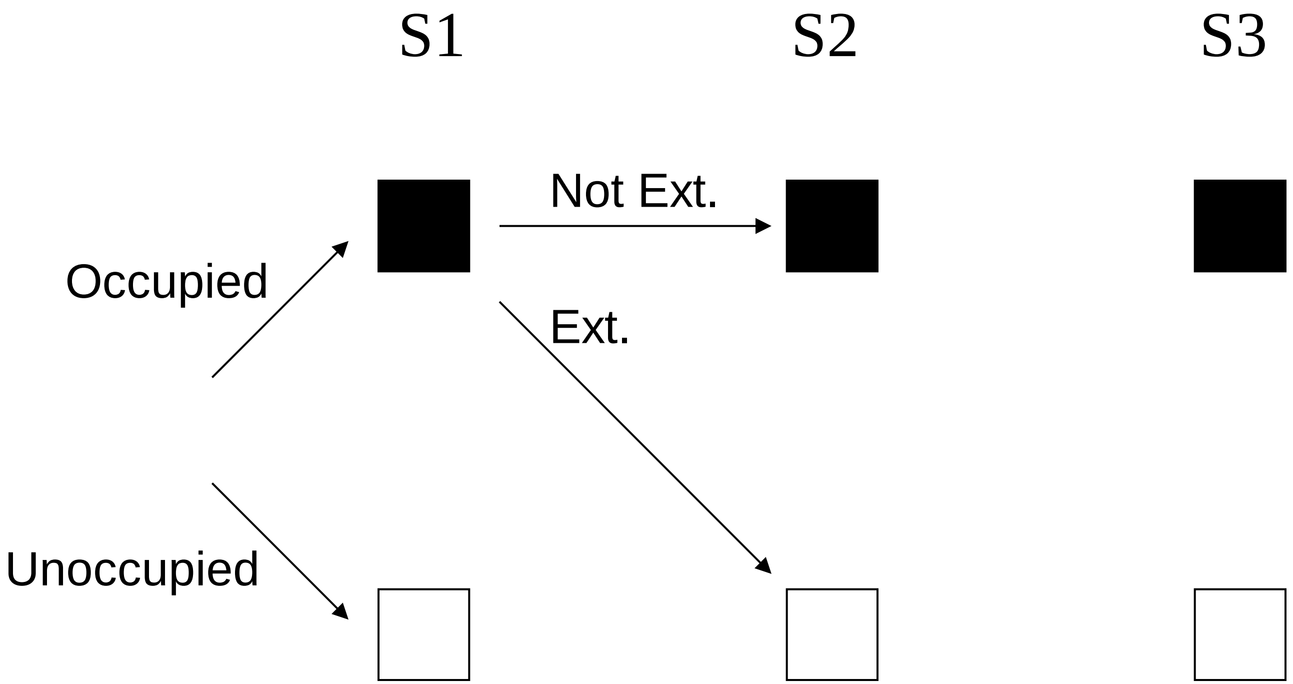

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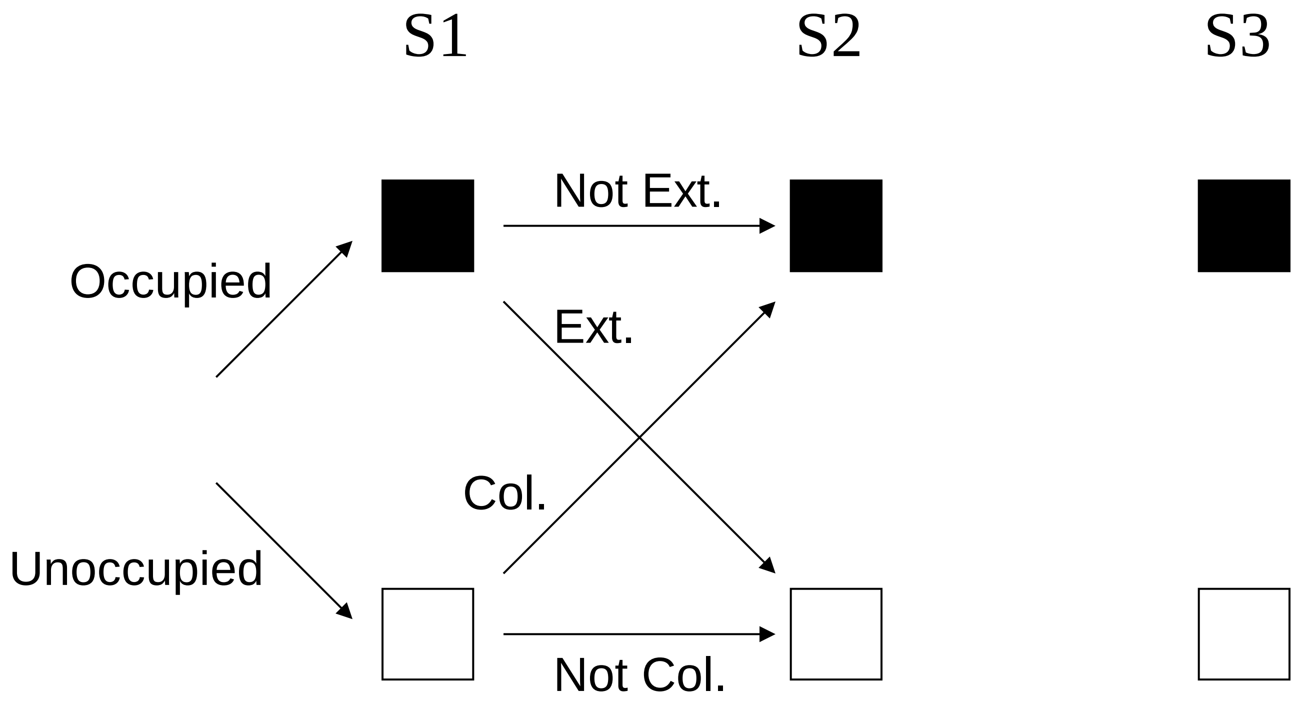

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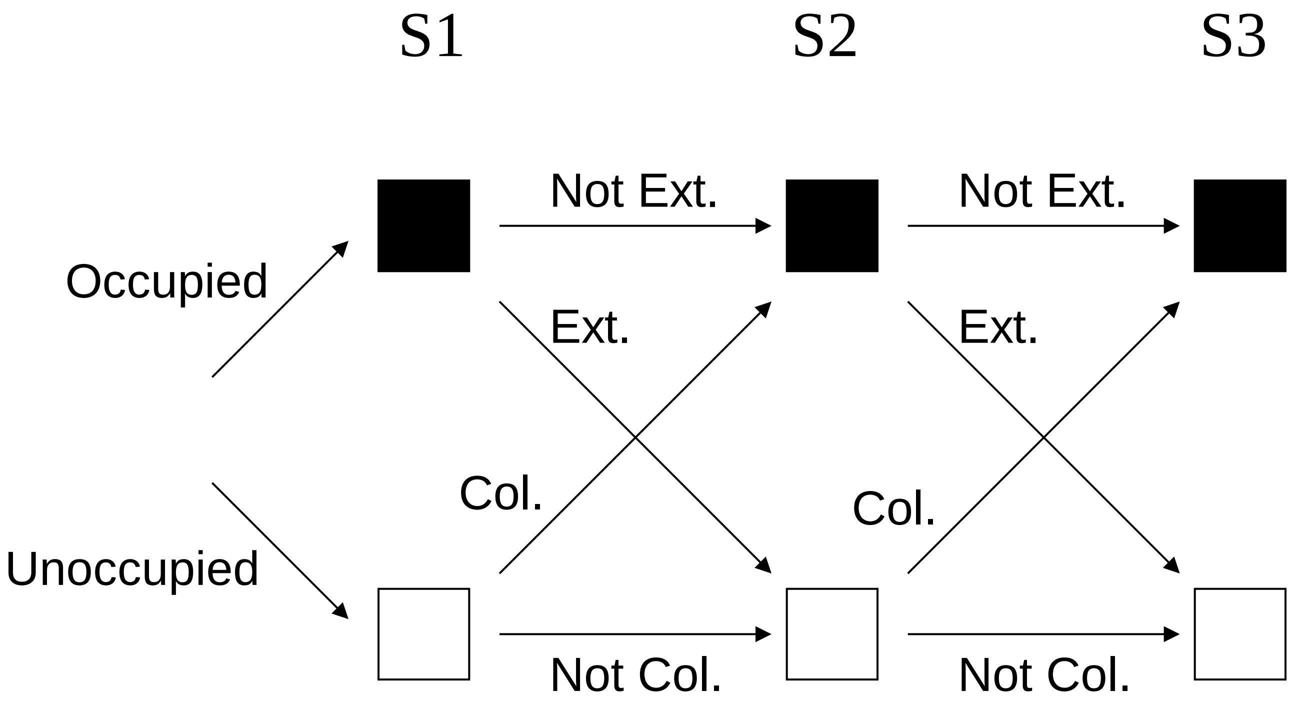


# Explicit Dynamics

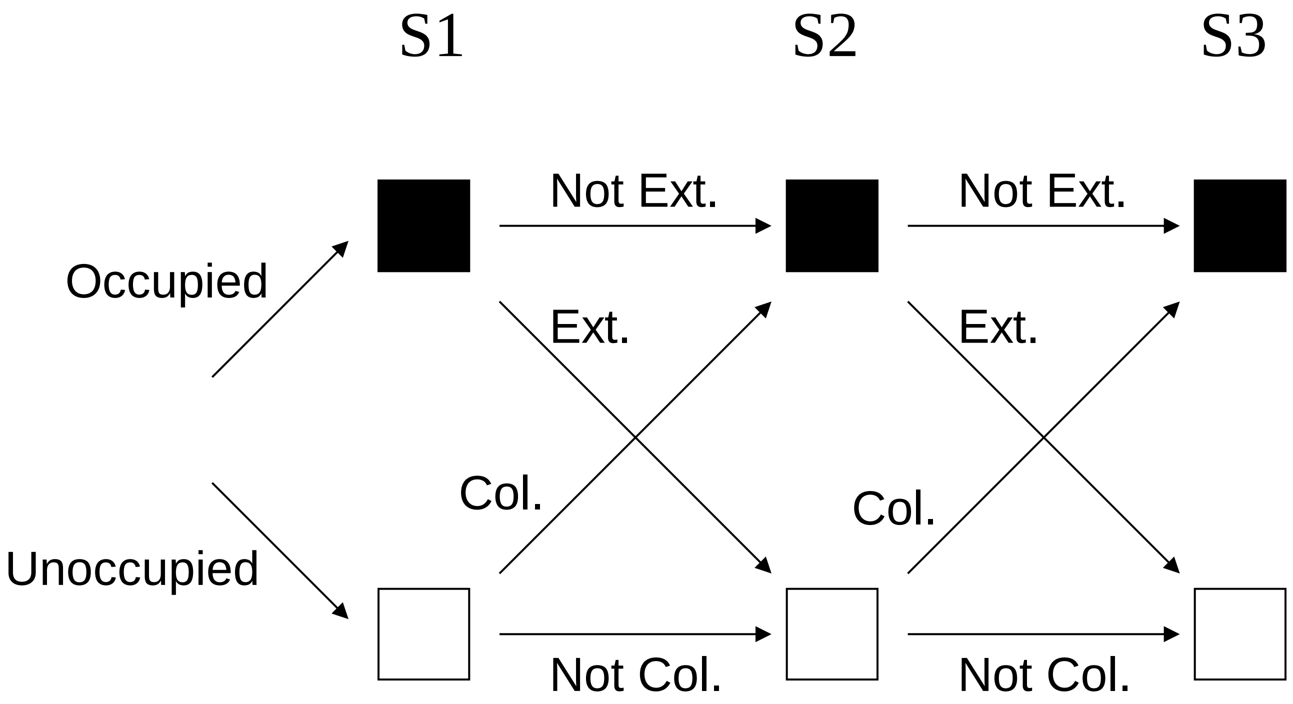
$\psi_1$ = probability unit occupied in season 1

$\varepsilon_t$ = probability a unit becomes unoccupied between seasons $t$ and $t+1$

$\gamma_t$ = probability a unit becomes occupied between seasons $t$ and $t+1$

$p_{t,j}$ = probability species detected at a unit in survey $j$ of season $t$ (given presence)

# Explicit Dynamics



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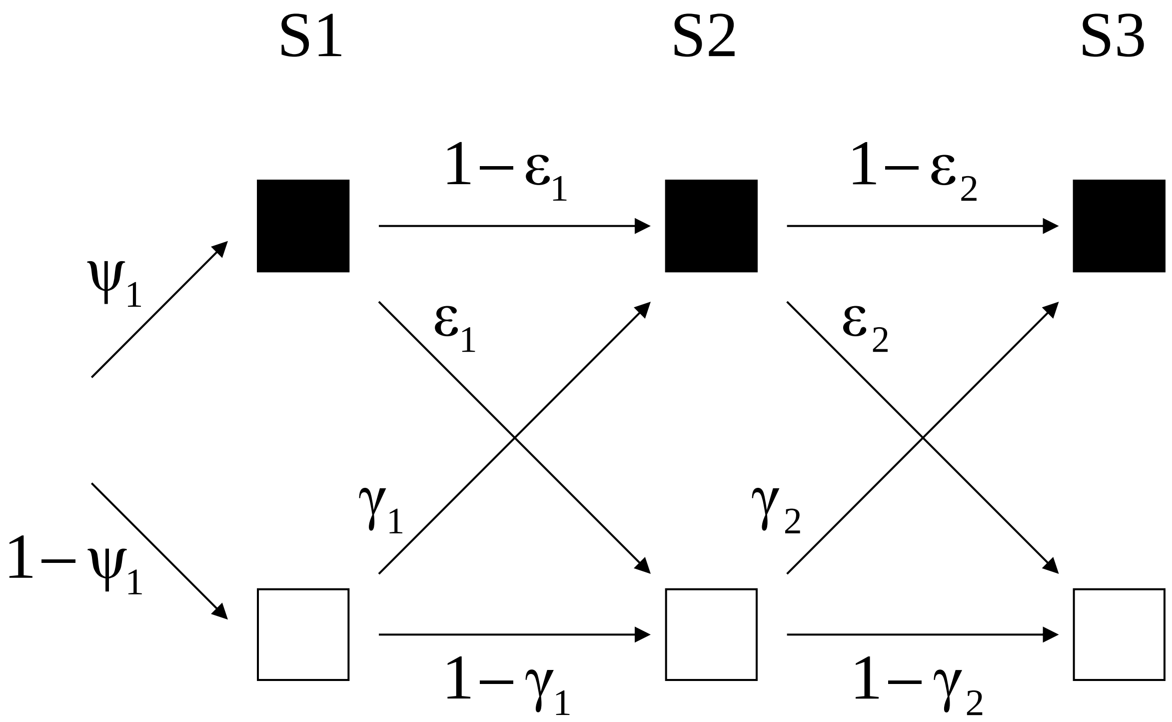

# Explicit Dynamics

- Complication is that species is detected imperfectly so can never be certain that a unit is unoccupied in any given season…

# Explicit Dynamics

For example,

$$\mathbf{h}_1 = 101\ 000$$

# Explicit Dynamics

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$$\mathbf{h}_1 = 101\ 000$$

Verbal description: species is present at the unit in season 1, was detected in first and third survey, not detected in second survey. Between seasons, species did not go locally extinct but was never detected in season 2, *OR* species did go locally extinct.

# Explicit Dynamics

For example,

$$\mathbf{h}_1 = 101\ \ 000$$

Mathematical translation:

$$\Pr\left(\mathbf{h}_1 = 101\,000\right) = \psi_1 p_{1,1}\left(1 - p_{1,2}\right) p_{1,3} \times$$

$$\left\{\left(1-\varepsilon_1\right)\prod_{j=1}^{3}\left(1 - p_{2,j}\right) + \varepsilon_1\right\}$$

# Explicit Dynamics

For example,

$$\mathbf{h}_2 = 000\ \ 010$$

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For example,

$$\mathbf{h}_2 = 000\ \ 010$$

Verbal description: species is present in season 1, but never detected, did not go locally extinct between seasons and was detected in the second survey. *OR* species was absent in season 1, colonized the unit between seasons and was detected in the second survey.

# Explicit Dynamics

For example,

$$\mathbf{h}_2 = 000\ \ 010$$

Mathematical translation:

$$\Pr\left(\mathbf{h}_2 = 000\ 010\right) = \left\{\psi_1 \prod_{j=1}^{3}\left(1 - p_{1,j}\right)\left(1 - \varepsilon_1\right) + \left(1 - \psi_1\right)\gamma_1\right\}$$

$$\times\left(1 - p_{2,1}\right) p_{2,2}\left(1 - p_{2,3}\right)$$

# Explicit Dynamics

- $\phi_t$ is the matrix of transition probabilities between occupied and unoccupied states between seasons $t$ and $t+1$

$$\phi_t = \begin{bmatrix} \mathrm{U} \rightarrow \mathrm{U} & \mathrm{U} \rightarrow \mathrm{O} \\ \mathrm{O} \rightarrow \mathrm{U} & \mathrm{O} \rightarrow \mathrm{O} \end{bmatrix}$$

$$\phi_0 = \begin{bmatrix} 1-\psi_1 & \psi_1 \end{bmatrix} \qquad \phi_t = \begin{bmatrix} 1-\gamma_t & \gamma_t \\ \varepsilon_t & 1-\varepsilon_t \end{bmatrix}$$

# Explicit Dynamics

- $\mathbf{p}_{\mathbf{h}t}$ is the vector of probabilities for an observed history in season $t$, conditional upon each occupancy state

$$\mathbf{p}_{\{101\}t} = \begin{bmatrix} 0 \\ p_{t1}\left(1 - p_{t2}\right) p_{t3} \end{bmatrix} \quad \mathbf{p}_{\{000\}t} = \begin{bmatrix} 1 \\ \prod_{j=1}^{3}\left(1 - p_{tj}\right) \end{bmatrix}$$

# Explicit Dynamics

- Generally,

$$\Pr\left(\mathbf{h}_i\right) = \phi_0 \prod_{t=1}^{T-1} D\left(\mathbf{p}_{\mathbf{h}_{it},t}\right) \phi_t \mathbf{p}_{\mathbf{h}_{iT},T}$$

where, $D(\mathbf{Y})$ is a diagonal matrix with the elements of $\mathbf{Y}$ on the main diagonal.

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where, $D(\mathbf{Y})$ is a diagonal matrix with the elements of $\mathbf{Y}$ on the main diagonal.

- $ODL\left(\boldsymbol{\theta}\middle|\mathbf{h}\right) = \prod_{i=1}^{s} \Pr\left(\mathbf{h}_i\right)$

# Explicit Dynamics

- Alternatively could specify the complete data likelihood.

$$CDL\left(\boldsymbol{\psi}_1,\boldsymbol{\gamma},\boldsymbol{\varepsilon},\mathbf{p}\,\middle|\,\mathbf{h},\mathbf{z}\right)=\prod_{i=1}^{s}\left[\begin{array}{c}\psi_1^{z_{1i}}\left(1-\psi_1\right)^{1-z_{1i}}\\ \times\prod_{t=1}^{T-1}\left[\gamma_t^{z_{t+1i}}\left(1-\gamma_t\right)^{1-z_{t+1i}}\right]^{1-z_{ti}}\\ \times\prod_{t=1}^{T-1}\left[\left(1-\varepsilon_t\right)^{z_{t+1i}}\varepsilon_t^{1-z_{t+1i}}\right]^{z_{ti}}\\ \times\prod_{t=1}^{T}\left[\prod_{j=1}^{k}p_{tj}^{h_{tij}}\left(1-p_{tj}\right)^{1-h_{tij}}\right]^{z_{ti}}\end{array}\right]$$

# Implicit vs. Explicit Dynamics?

- When a small fraction of the units are continually surveyed, the implicit dynamics approach may be more numerically reliable.

- Implicit model only models *patterns* in occupancy each season, or assumes changes in occupancy are random.

# Either Approach

- Probabilities could be functions of covariates.

- Allow for missing values, both individual surveys and for entire seasons.

# Example

Grand skinks (*Oligosoma grande*) near Macraes Flat, Otago, NZ

Photo: Catherine Roughton, University of Otago


GOLD MEDAL ALE

# The data

- Rock outcrops surveyed by DOC up to 3 times per year.
- 5-year period with 338 outcrops.
- Interested in colonisation and extinction probabilities, and whether they differ between areas of tussock and pasture.

# The results

Fit 2 models:

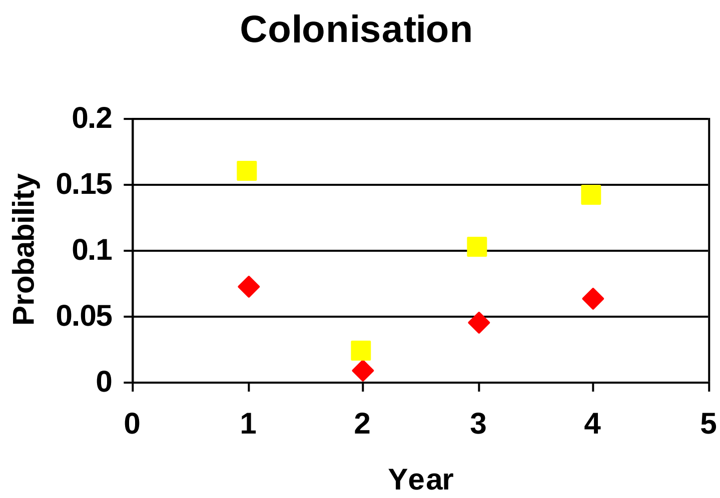
$\psi(H)\gamma(t+H)\varepsilon(t+H)\,p(t)$ vs. $\psi(H)\gamma(t)\varepsilon(t)\,p(t)$

$\Delta$AIC >7 in favour of the former model

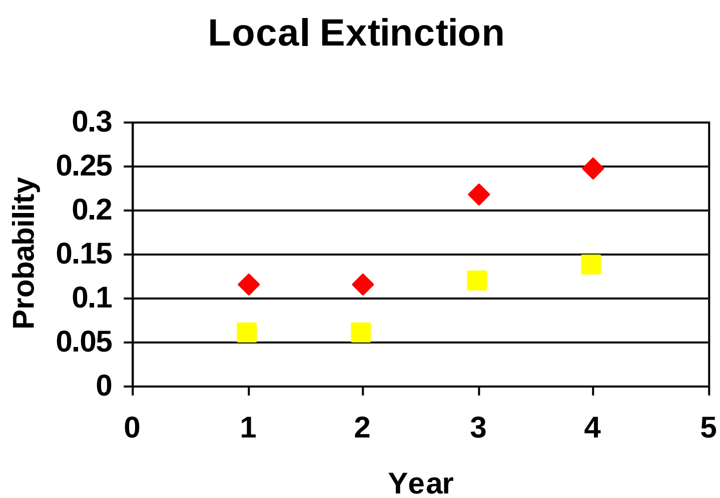
Odds ratio for an outcrop surrounded by pasture;

a) being colonized is 0.4 (0.2, 0.9)

b) going locally extinct is 2.1 (1.0, 4.4)




farm pasture
Native grassland



# Multiple Season Model

Part II

# Explicit Dynamics: Alternative Parameterizations

- Initial parameterization: $(\psi_1, \varepsilon_t, \gamma_t)$

- Complement of local extinction is local survival or persistence:

$$\phi_t = 1 - \varepsilon_t$$

- Alternative parameterization: $(\psi_1, \phi_t, \gamma_t)$

# Explicit Dynamics: Alternative Parameterizations

- Colonization =

  Pr(occupied at $t$+1|unoccupied at $t$)

$$\gamma_t = \psi_{t+1}^{[0]}$$

- Persistence =

  Pr(occupied at $t$+1|occupied at $t$)

$$\phi_t = 1 - \varepsilon_t = \psi_{t+1}^{[1]}$$

# Explicit Dynamics: Alternative Parameterizations

- Estimating occupancy at $t>1$

$$\psi_{t+1} = \psi_t(1-\varepsilon_t) + (1-\psi_t)\gamma_t$$

- Alt. parameterizations: $(\psi_t, \varepsilon_t)$, $(\psi_t, \gamma_t)$

- Occupancy growth rate:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}$$

- Alt. parameterizations: $(\psi_1, \varepsilon_t, \lambda_t)$, $(\psi_1, \gamma_t, \lambda_t)$

# Explicit Dynamics: Alternative Parameterizations

- Previous definition for growth rate not entirely satisfactory, alternatively:

$$\lambda_t^* = \frac{\psi_{t+1}/(1-\psi_{t+1})}{\psi_t/(1-\psi_t)}$$

$$\operatorname{logit}(\psi_{t+1}) = \beta_0 + \sum_{j=1}^{t} \beta_j$$

$$\lambda_t^* = e^{\beta_t}$$

- If $\lambda_t^* = \lambda^*$ then: $\operatorname{logit}(\psi_{t+1}) = \beta_0 + \beta_1 t$

$$\lambda^* = e^{\beta_1}$$

# Explicit Dynamics: Alternative Parameterizations

- ‘Turnover’ of occupied units may be of interest.

- $\tau_t$ = Pr (occupied site at $t$+1 is a newly occupied site).

$$\tau_t = \frac{(1-\psi_t)\gamma_t}{\psi_{t+1}}$$

- Can also estimate $\tau_t$ directly as local extinction from reverse-time analysis.

- Alt. parameterizations: $(\psi_1, \tau_t, \varepsilon_t)$, $(\psi_1, \tau_t, \gamma_t)$

# Explicit Dynamics: Alternative Parameterizations

- Selection: based on parameters about which direct inference and covariate modeling are of primary interest.
  - What's your study objective again?

- But, generally focusing on 'trends' may not be that informative. Understanding why a trend is occurring frequently requires knowledge about the underlying dynamics.
  - Why is there a downwards trend? High level of extinction or low level of colonization?

# Example: House Finch Expansion in North America

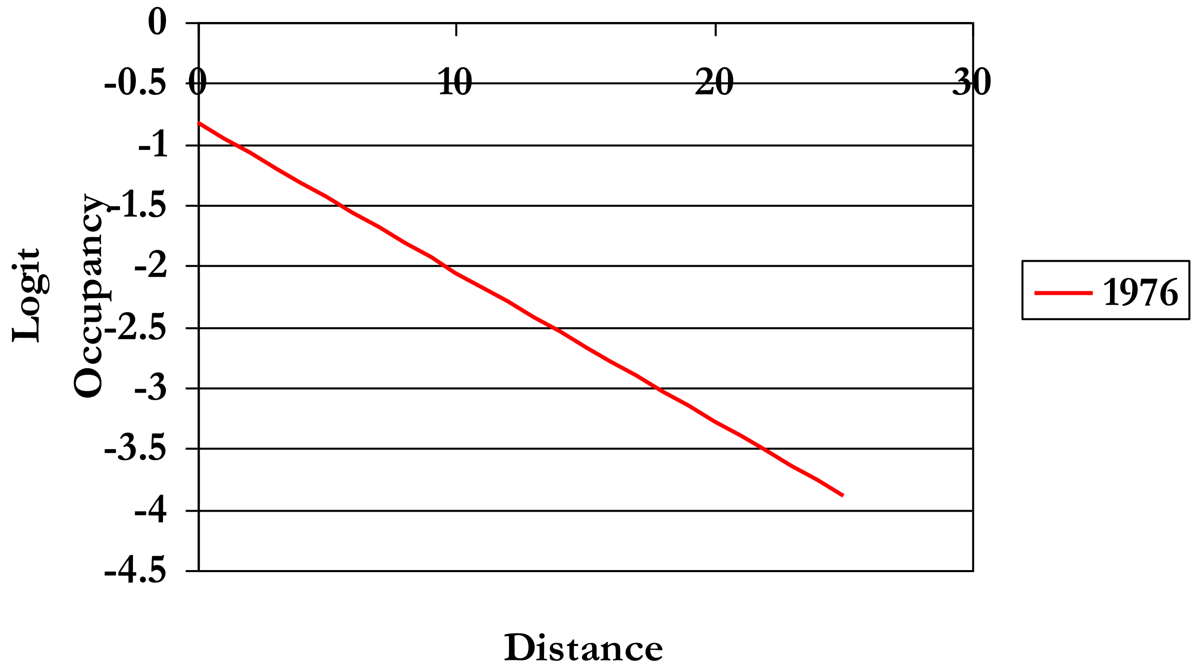
- Native to south-west US and Mexico.
- Released in Long Island, NY in 1940's.
- Model expansion of species range from 1976-2001 using BBS data.

# The data

- Each BBS route is considered the sampling unit.
- The 50 stops along the route represent our repeated surveys.
- Distance from release point (measured in 100km bands) was considered as a covariate for all parameters.
- The covariate ‘f’ was defined for detection probability to =1 if HF detected at >10 stops at that route in a previous year, 0 otherwise.

# Results

- After some model selection, the model $\psi_{76}(d)\gamma(year*d)\varepsilon(d)p(year*d+f)$ was ranked best.



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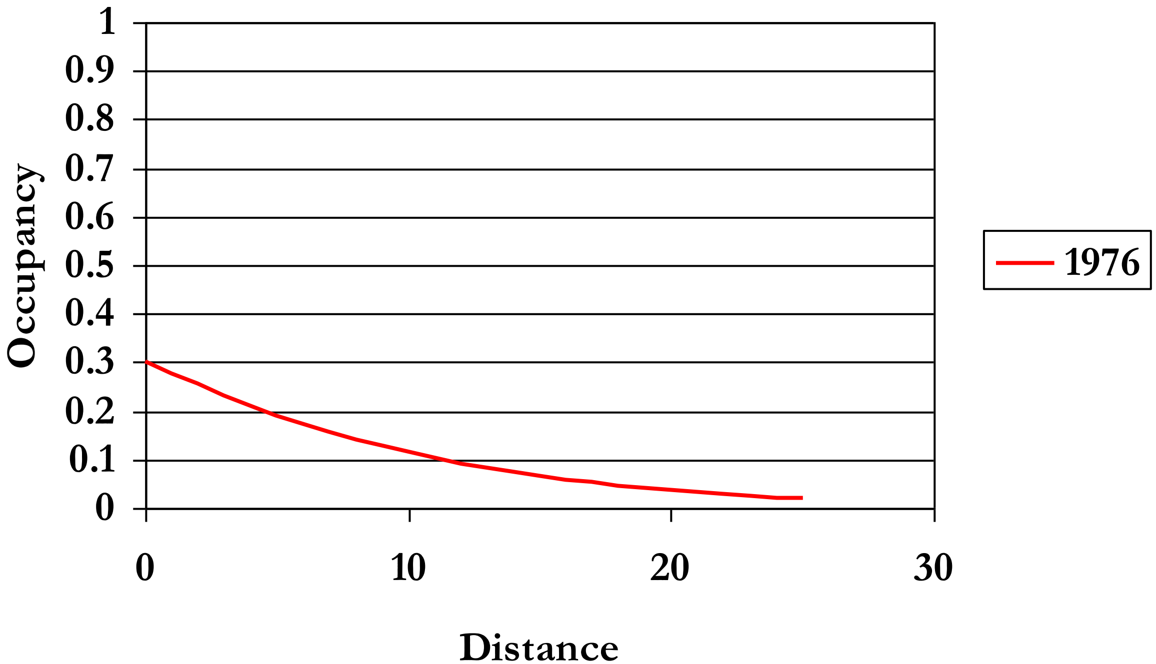

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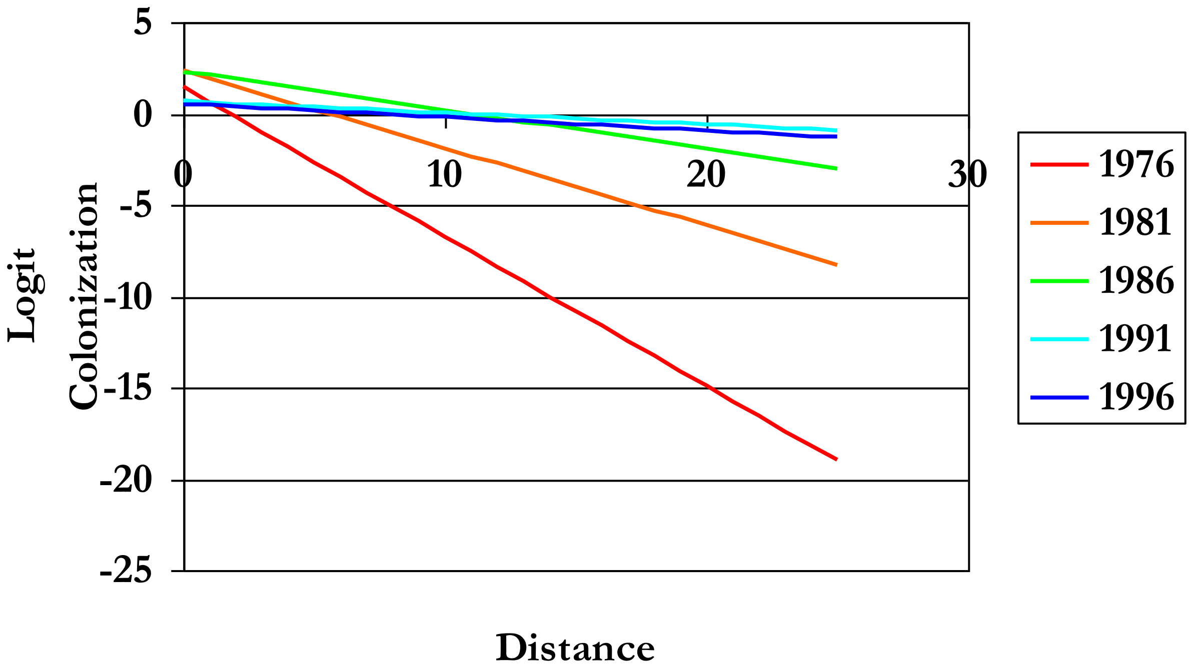

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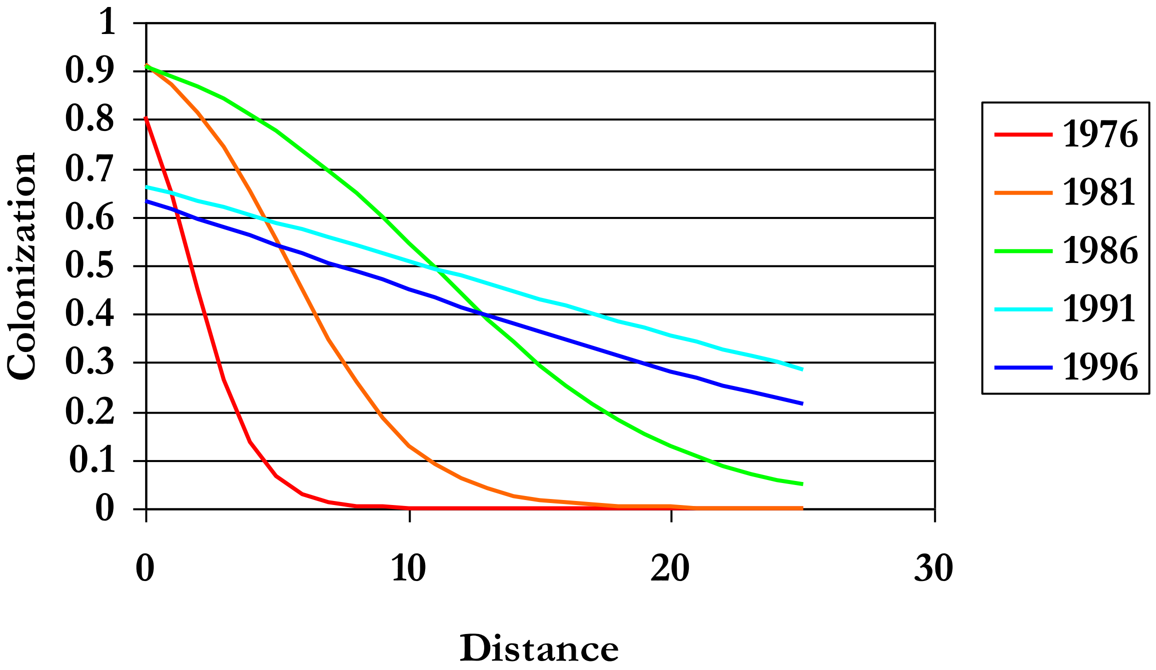

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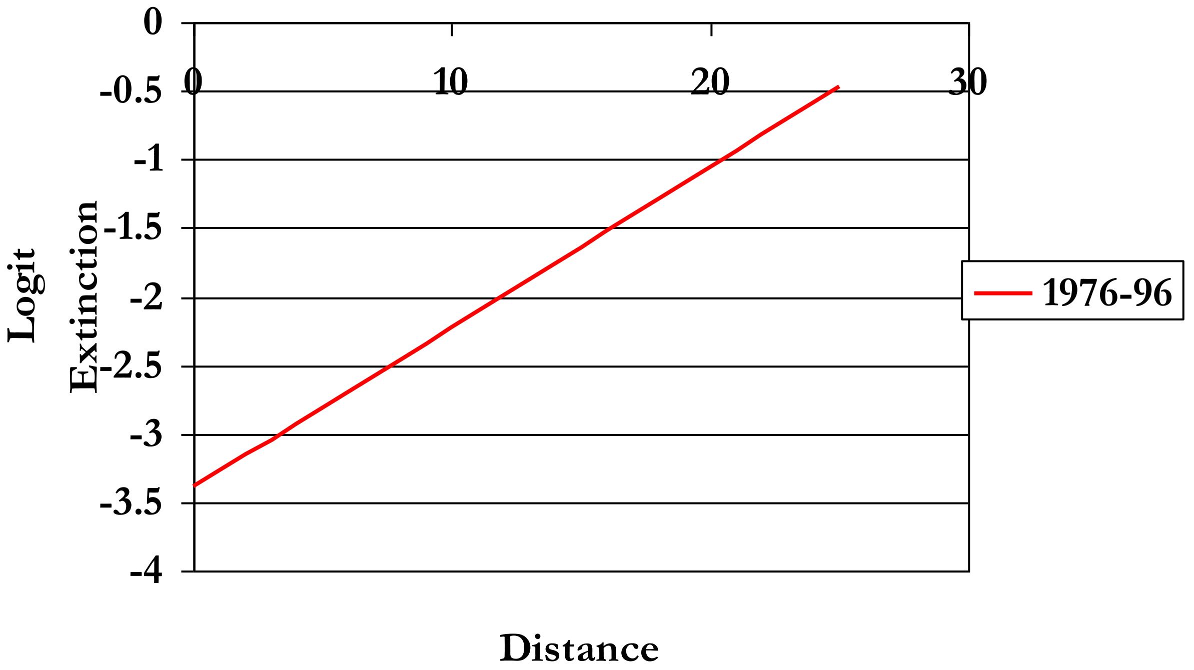

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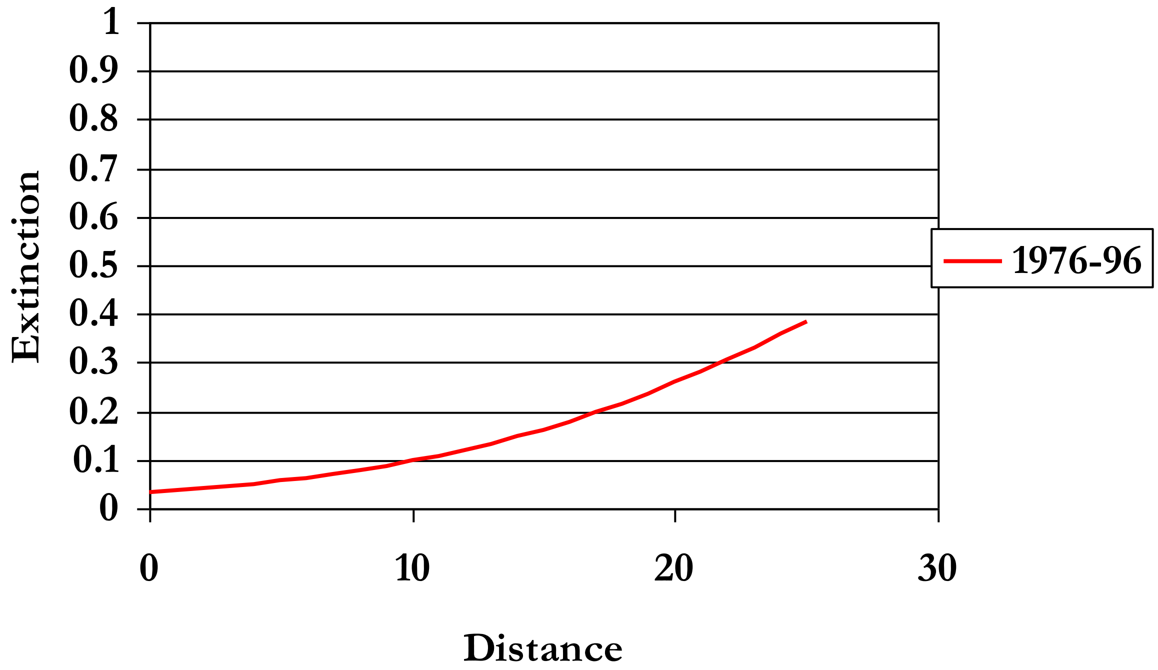

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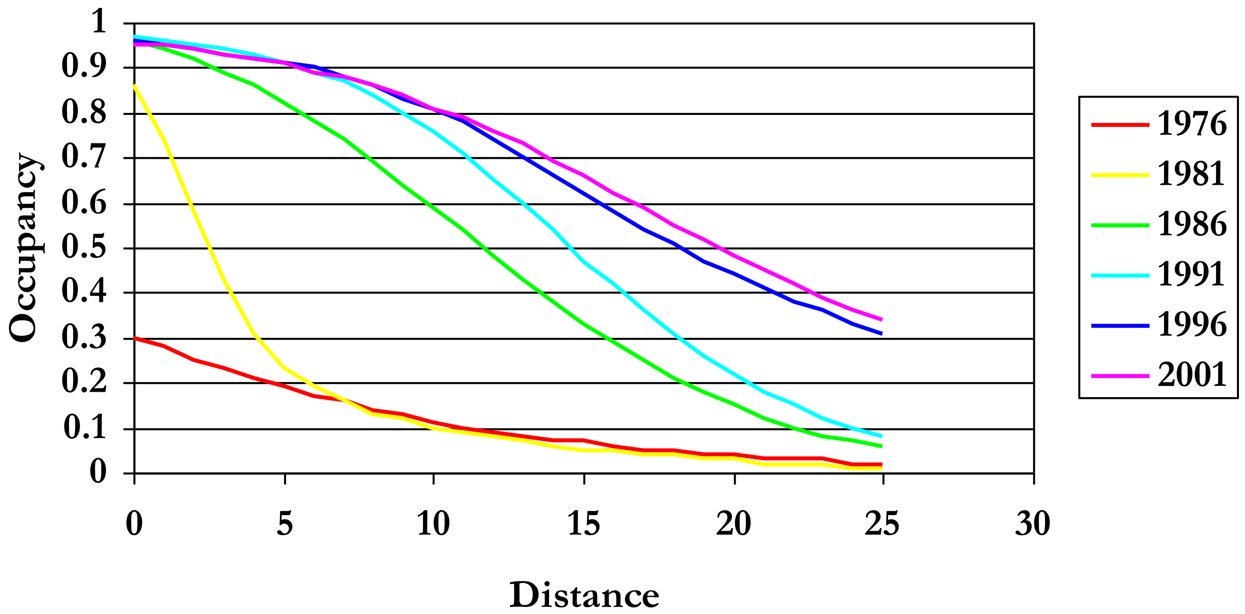

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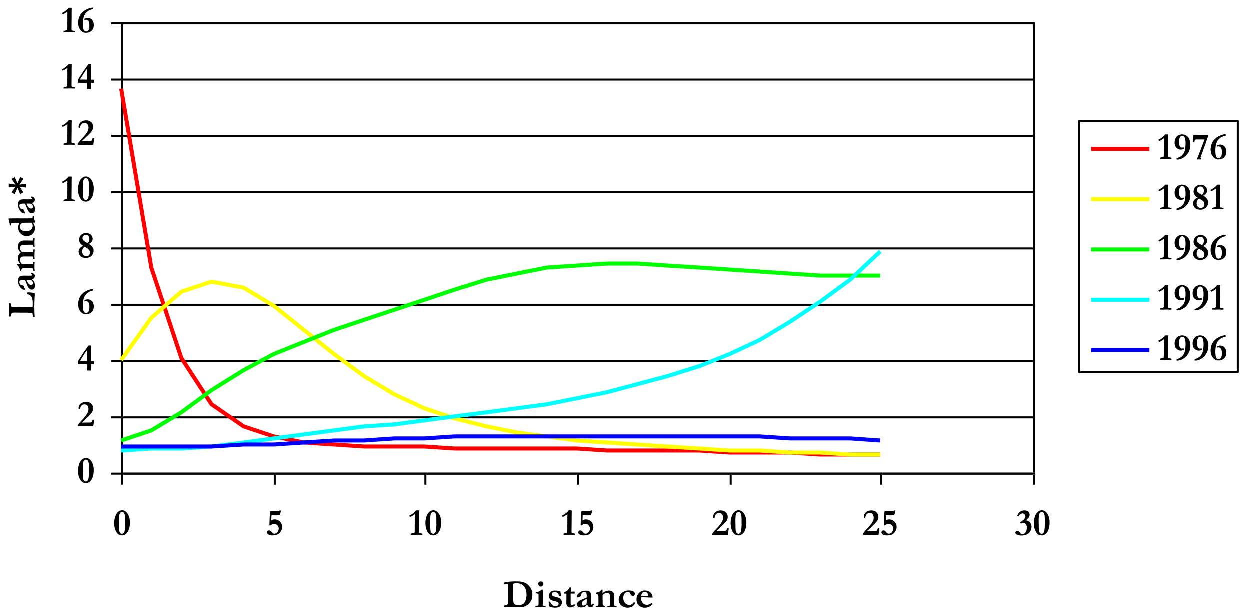


# Characterizing the Processes Underlying Occupancy Dynamics

- How does the occupancy status of units change over time?
  - Markovian dynamics (i.e., $\gamma_t$, $\varepsilon_t$; explicit model)
  - Random dynamics (i.e., $\gamma_t = 1 - \varepsilon_t$; implicit model)
  - No change (i.e., $\gamma_t = \varepsilon_t = 0$)
- Each of these models can be fit to the data and formally compared

# Characterizing the Processes Underlying Occupancy Dynamics

- Random dynamics

$$\phi_t = \begin{bmatrix} 1-\gamma_t & \gamma_t \\ \varepsilon_t & 1-\varepsilon_t \end{bmatrix} = \begin{bmatrix} 1-\gamma_t & \gamma_t \\ 1-\gamma_t & \gamma_t \end{bmatrix}$$

$$\begin{aligned} \psi_{t+1} &= \psi_t \gamma_t + (1-\psi_t)\gamma_t \\ &= \psi_t \gamma_t + \gamma_t - \psi_t \gamma_t \\ &= \gamma_t \end{aligned}$$

# Characterizing the Processes Underlying Occupancy Dynamics

- Is the population at equilibrium?

  (1) Can probability of occupancy be modeled as constant over time

  Model comparison: $\psi_t$ vs. $\psi_.$

  (2) Are the vital rates constant over time (i.e., is it a stationary Markov process)

  Model comparison: $\varepsilon_t, \gamma_t$ vs. $\varepsilon, \gamma$

- These 2 concepts of equilibrium not equivalent (compensating vital rates, transient dynamics)

- Equilibrium occupancy: $\psi^* = \dfrac{\gamma}{\gamma + \varepsilon}$

# Perturbation Analysis

- Purpose: to assess sensitivity of a system state variable or related quantity to changes in system rate parameters

- Equilibrium occupancy, $\psi^*$, reflects system well-being for patch occupancy models and can be viewed in same manner as asymptotic $\lambda$ of population projection models

- Develop expressions for sensitivity of $\psi^*$ to changes in probabilities of local extinction and colonization

# Sensitivities for Equilibrium Occupancy

$$\psi^* = \frac{\gamma}{\gamma + \varepsilon}$$

$$s_\gamma = \frac{\partial \psi^*}{\partial \gamma} = \frac{\varepsilon}{(\gamma + \varepsilon)^2}$$

$$s_\varepsilon = \frac{\partial \psi^*}{\partial \varepsilon} = -\frac{\gamma}{(\gamma + \varepsilon)^2}$$

# Sensitivities for Patch Occupancy Models: Intuition

- Prediction: sensitivity should be greatest for the parameter that applies to the larger number of patches (occupied or unoccupied)

- Results:

$$\psi^* > 0.5 \Rightarrow \left|s_\varepsilon\right| > \left|s_\gamma\right|$$

$$\psi^* < 0.5 \Rightarrow \left|s_\gamma\right| > \left|s_\varepsilon\right|$$

$$\psi^* = 0.5 \Rightarrow \left|s_\varepsilon\right| = \left|s_\gamma\right|$$

# Golden Eagles at Denali National Park, Alaska

- 1988-2007, April-May, C. McIntyre surveyed potential golden eagle territories (by helicopter, foot) up to 3 times
- Removal occupancy design (stop at first detection)
- Fit models reflecting different hypotheses about existence of dynamic equilibrium

## Model selection of patch occupancy models for Golden Eagles in Denali National Park.

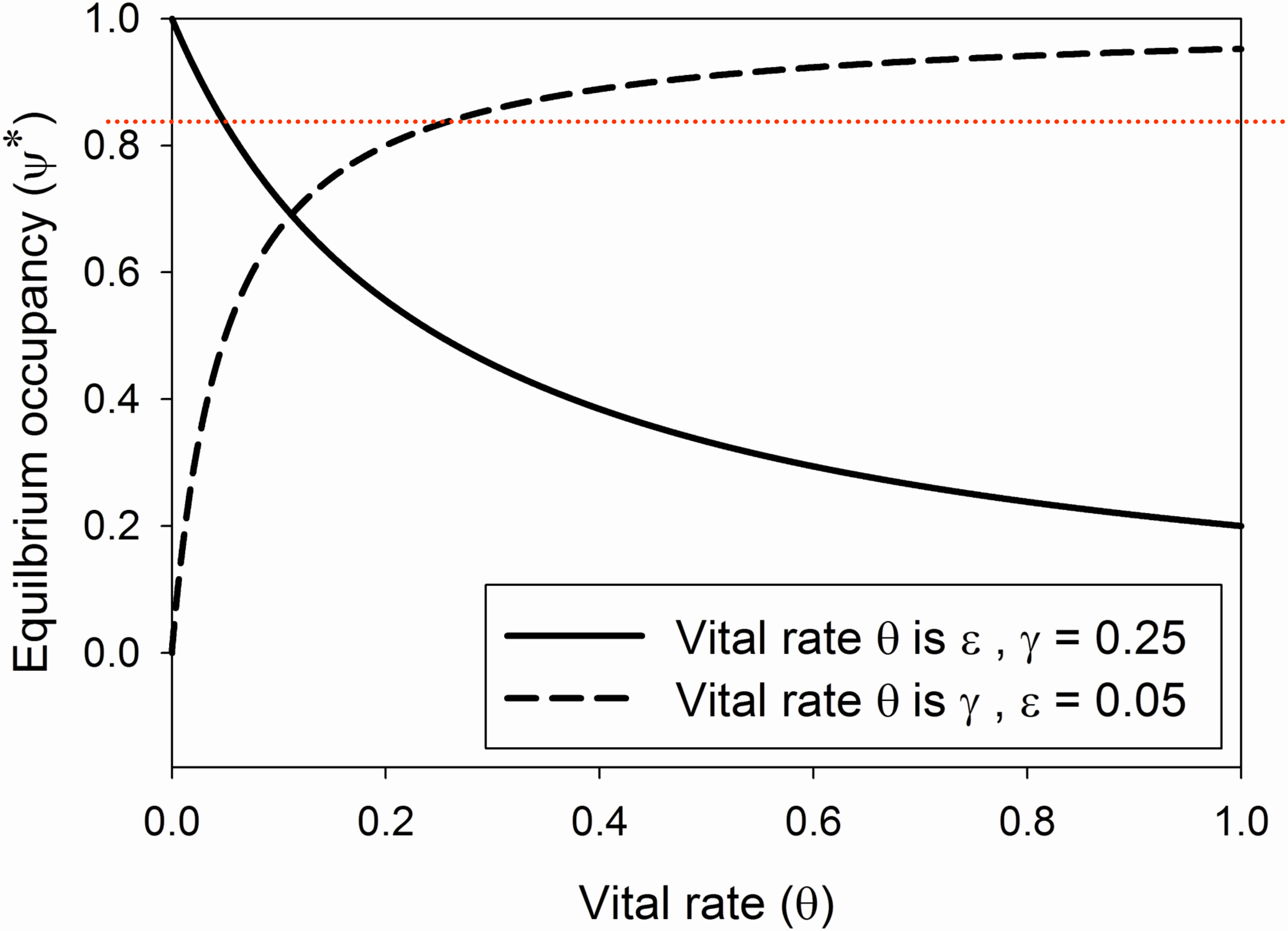
| Model | AIC | ΔAIC | K |
|---|---|---|---|
| $\psi_{1-20}(.)\varepsilon(.)\,p(yr)$ | 1157.1 | 0 | 22 |
| $\psi_1(.)\varepsilon(.)\gamma(.)\,p(yr)$ | 1158.1 | 1 | 23 |
| $\psi_1(.)\varepsilon(.)\gamma(.)\,p(.)$ | 1160.0 | 2.9 | 3 |
| $\psi_1(.)\varepsilon(yr)\gamma(.)\,p(yr)$ | 1173.6 | 16.5 | 41 |
| $\psi_1(.)\varepsilon(.)\gamma(yr)\,p(yr)$ | 1174.7 | 17.6 | 41 |
| $\psi_1(.)\varepsilon(yr)\gamma(yr)\,p(yr)$ | 1193.5 | 36.4 | 59 |

*Notes:* AIC: Akaike information criterion. ΔAIC for the ith model is computed as $AIC_i$ - min (AIC). K: number of parameters.

# Occupancy Modeling Results

- Support for hypothesis of equilibrium (constancy of occupancy and rate parameters)

- Estimates
  - Colonization: $\hat{\gamma} = 0.25 \ \ (S\hat{E} = 0.026)$
  - Extinction: $\hat{\varepsilon} = 0.05 \ \ (S\hat{E} = 0.006)$
  - Equilibrium occupancy: $\hat{\psi}^* = 0.83$
  - Sensitivities: $\hat{s}_{\varepsilon} = -2.8$ $\hat{s}_{\gamma} = 0.6$



Equilbrium occupancy (ψ*)
1.0
0.8
0.6
0.4
0.2
0.0
Vital rate θ is ε , γ = 0.25
Vital rate θ is γ , ε = 0.05
0.0
0.2
0.4
0.6
0.8
1.0
Vital rate (θ)

# Sensitivities for Equilibrium Occupancy: Considerations and Insights

- Colonization is especially important for rare species (low $\psi^*$)
- Extinction is the more important process for common species (high $\psi^*$)
- Sensitivities are relevant to management, but are not the whole story:

$$\frac{\partial \psi^*}{\partial \theta} \frac{\partial \theta}{\partial x} \frac{\partial x}{\partial y}$$

  - $x$ = management action
  - $y$ = unit cost for management actions
  - $\theta$ = vital rate

# Finite Population

- As for the single season situation, could use the data augmentation approach to predict the occupancy state of each unit each season.

- Make inference about the *proportion* of sites occupied in the sample, or some other relevant summary of occupancy dynamics.

# Summary

- Multi-season models allow us to make inference about changes in occupancy and the underlying dynamic processes.

- A suite of flexible methods is now available that account for:
  - detectability
  - covariates
  - unequal sampling effort
  - different types of dynamics
  - finite populations
  - spatial correlation

- We believe that in the future much greater emphasis will be placed on understanding the dynamics of species occurrence.